EFFECT OF URBANIZATION ON THE SURVIVAL AND MOVEMENTS OF LOCALIZED POPULATIONS OF WHITE-TAILED DEER IN SOUTHERN INDIANA

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ABSTRACT

TITLE: Effect of Urbanization on the Survival and Movements of Localized Populations of White-tailed Deer in Southern Indiana.

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In recent decades, the effects of urbanization on White-tailed deer (*Odocoileus virginianus*) (hereafter WTD) populations have become a major area of interest to wildlife professionals. However, while a fair amount of studies have compared the population dynamics of urbanized WTD populations (such as movement and survival) on a broad scale, few if any have ever attempted to compare them to a population along a localized gradient at the same place and time. Although the population dynamics of urbanized WTD seem to be consistent throughout literature, management applications may be undermined by inaccurate perceptions of how urban WTD populations respond when applications are based on conclusions from varying populations. By comparing common population dynamics such as movement and survival between adjacent groups of urban and rural WTD within the same general area, biologists can more accurately evaluate the direct impacts of urbanization on WTD within localized populations. This study was conducted in two counties in southern Indiana: Monroe and Brown. The city of Bloomington, Indiana has a healthy population of urban deer. We free darted WTD

from a distance or captured them using dropnets, Clover traps, or suspended net guns. Once immobilized, WTD were equipped with GPS or VHF collars and monitored using satellite or radio telemetry to obtain location data. From January-July 2015-16 a total of 85 WTD was captured consisting of 45 urban individuals and 40 rural individuals. We used Kaplan-meier known fates models to determine survival and dispersal probabilities and occupancy models to determine excursion probability. Parameters of the models were estimated using Bayesian inference in JAGS. Covariates used in model selection included locality, season, and sex. Overall, survival rates were positively correlated between sex and season but not locality. Dispersals were predominately undertaken by males (25% of collared bucks), however they were not positively correlated by season or locality. Our results also suggest that urban WTD were less likely to be observed while on an excursion across all seasons than their rural counterparts, however the influence of sex did not affect excursion probability. Furthermore, both localities had highest excursion probabilities during the fall/winter and winter/spring seasons compared to the summer.

DEDICATION

I dedicate this work to my papaw…if he would have never taken me fishing, I question whether I would have ever done this.

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CHAPTER 1

LITERATURE REVIEW

DISTRIBUTION

White-tailed deer (*Odocoileus virginianus*, hereafter WTD) are recognized as being the most widely distributed New World cervid species, with a native range spanning from northwestern Canada to central South America (Heffelfinger 2011). Additionally, there have been many introduction attempts that have taken place over the last century including: New Zealand, Finland, the British Isles, Austria, Czech Republic, Slovakia, Serbia, Croatia, Bulgaria, Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands, and various islands of the West Indies (Heffelfinger 2011). The WTD has adapted to virtually every habitat type occurring across its range, typically limited only due to severe winters within boreal regions (Heffelfinger 2011). However, boreal regions could be improving winter inhabitability for WTD due to recent increases in forestry practices as well as agricultural expansion.

While characteristic overlap is commonplace across most of its range, there are currently 38 unique WTD subspecies. Furthermore, many others have been previously described but lacked validity due to insufficient samples (Heffelfinger 2011). Many of these subspecies have come about as examples of phenotypic plasticity where populations share similar features because of adaptations to unique habitats while others share characteristics based on genetic isolation (Strickland and Demarais 2000, 2008). Many populations have experienced human-induced genetic variation because of restocking efforts (Marchinton et al. 1995).

POPULATION DYNAMICS

The population dynamics of free ranging WTD have fluctuated drastically throughout its existence. The species has persisted through various prehistoric eras in which competition and large predator abundance could have potentially brought the species to extinction (Owen-Smith 1987, Haynes 1983). Now considered a "keystone species"; ecosystems can be drastically altered by higher densities of a WTD populations within them (Molvar et al. 1993, Wallis de Vries 1995, Hobbs 1996, Bowyer et al. 1997, Simberloff 1998, Kie et al. 2002, 2003). This concept becomes a critical management concern when considering the reproductive potential of WTD. Foundational WTD fecundity studies have documented rates of population increase as high as 89% when a herd is occupying a favorable habitat (McCullough 1979, Downing and Guynn 1985). Under these conditions, many fawns often reach puberty and are bred within their first year of life (Ozoga 1987) and it is not uncommon for females to average greater than 2 fetuses per litter (Haugen 1975, Dapson et al. 1979).

Mortality rates in WTD are highly variable depending on region, habitat type, sex, and age class. Prenatal mortality is usually quite low in WTD as most previous studies have documented under 15% (DeYoung 2011). Mortality typically tends to be lower post six months of age but can still be strongly influenced by hunter harvest (DeYoung 2011). In the Midwest hunting related mortality has been as low as 2.6% for yearling does in Illinois (Nixon et al. 1991) to as high as 47% in yearling bucks in Michigan (Van Deelen et al. 1997). Furthermore, mortality has also been documented as a "U-shaped" curve in males; where highest rates of mortality occur at ≤ 3 months, greatly decrease, then spike again exponentially at 109-120 months (DeYoung 1989). This can primarily be attributed to hunters selecting for more mature males with larger

antler characteristics. As a whole, WTD survivorship is typically lower for neonates and higher for adults (Gaillard et al. 2000). Nonetheless, previous literature shows that non-hunting related mortality rates are typically very low regardless of sex but can be influenced by old age (Nelson and Mech 1990).

While populations can be altered by both density dependent and density independent factors, most management strategies tend to focus on density dependent responses and the measures needed to better understand the nutritional carrying capacity (NCC) within a certain population (Bishop et al. 2009). Over the years, predictive models have been used to give managers a better sense of how population estimates can be kept at an appropriate level to compensate for a variety of density dependent factors, primarily hunter harvest (DeYoung et al. 2008). These strategies are centered around managing density dependent interactions in a manner which allows the population to reach a certain level of abundance prior to NCC. At this desired population size known as maximum sustained yield (MSY), the herd is consistently growing at the most efficient rate possible while still retaining an adequate level of habitat quality. It is at this point that the herd can sustain the highest level of compensatory mortality without negatively affecting its overall health.

HOME RANGE

Investigation of spatial home ranges is one of the most studied aspects of WTD biology and management. This can be attributed to the idea that home range serves as the only primary index of space use by wildlife (Hemson et al. 2005). A home range is defined as the area an animal utilizes to meet its needs for food, water, cover, social

interactions, and caring for young (Burt 1943, Stewart et al. 2011). Home ranges are typically estimated by repeatedly collecting geographic locations on individuals over a set period of time before quantifying the overall area of space use.

Like many other ungulate species, home range estimates of WTD can vary greatly depending on a plethora of biological variables. In general, most studies tend to favor the assumption that WTD occupying higher quality habitats have smaller home ranges than those living in sparsely suitable habitats (Marchinton and Hirth 1984). However, estimates can fluctuate based on the type of home range being analyzed (i.e. season vs. annual). Seasonally, home range size is often variable due to changes in food and water availability. During the winter months WTD home ranges are often influenced by a lack of mobility to conserve energy (Moen 1976, Parker et al. 1984). Many northern studies have found that during these months WTD will congregate in localized wintering areas known as "yards" in efforts to fulfill home range requirements (Telfer 1967, Rongstad and Tester 1969). Conversely, other studies have found that wintering areas were more than double the size of summer home ranges. This is thought to be attributed agriculture fields which provide individuals with necessary means to survive without having to travel great distances to meet habitat demands during the summer months (Nixon et al. 1991, Brinkman et al. 2005). Furthermore, deer are an "edge species" in that they thrive in areas where habitat types are intermixed and directly adjacent to one another (Swift 1946, Williamson and Hirth 1985, Alverson et al. 1988).

Home range has been shown to be different between males and females. Previous literature states that males tend to have larger home ranges due to the need to occupy larger areas in order to meet nutritional requirements; especially during the late fall and

winter (Nicholson et al. 1997, Beier and McCullough 1990, Barbosa and Boyer 2000, 2001, Long et al. 2008). This is presumably linked to males typically having larger body sizes as well as having to compensate for increased energy expenditure during the breeding season (Nelson and Mech 1981, 1984). Females tend to shrink their home range as they near parturition in efforts to minimize interactions with other deer in order to care for their upcoming litters (Ozoga et al. 1982, Bertrand et al. 1996, D'Angelo et al. 2004). Likewise, both males and females tend to have larger home ranges during the winter and smaller home ranges during the spring and early summer (Marchinton and Hirth 1984).

MOVEMENT

Similar to home range research, the movement patterns of WTD have been studied extensively for years. However, many aspects within the topic are still some of the least understood within WTD biology and management (Bowman 2011, Diefenbach et al. 2008). This paucity of knowledge is somewhat counterproductive in that movement characteristics often give insight into many critical aspects of WTD management such as population dynamics, genetic flow, and disease transmission across a population (Diefenbach et al. 2008, Long et al. 2005, Nixon et al. 2007).

In order to maximize energy efficiency in meeting daily habitat requirements, WTD are widely considered to be crepuscular; meaning they exhibit most of their daily movements during the morning (typically at dawn) and evening (sunset) hours (Kammermeyer and Marchinton 1977, Ockenfels and Bissonette 1982, Rouleu et al. 2002, Webb et al. 2010). Furthermore, other studies have shown that of the two peak periods WTD tend to be more active at sunset than at dawn (Hosey 1980, Beier and

McCullough 1990). Other studies have found that WTD can fluctuate from being more active during crepuscular hours to having spikes of movement during diurnal hours (Naugle et al. 1997). Results on diurnal movement has typically found that deer tend to have spikes of activity between lull periods of inactivity while other studies have found there to be no pattern at all for mid-day movements (Beier and McCullough 1990, Demarais et al. 1989).

Movement rates are often strongly influenced by weather conditions, habitat variations, and seasonal behaviors associated with the onset of the fawning or the rut. Therefore, movement rates of bucks and does may vary depending on current biological responses that are associated with each season (DeYoung and Miller 2011). While females tend to have smaller home ranges as they approach parturition, their movement rates tend to increase in relation to meeting metabolic demands for them to successfully fawn. The increase in activity is essentially a response to compensate for the energy expenditure that is required for successful gestation and lactation (DeYoung and Miller 2011). A study by Beier and McCullough (1990) found does to be more active for 1.5 hrs/per day than bucks from the months of January to July. Males on the other hand typically tend to move the most during the rut; primarily in response to competition from other bucks and finding receptive does to breed (Rosenberry et al. 2001, Shaw et al. 2006, Hawkins and Klimstra 1970). One Oklahoma GPS study found bucks to move an average 7.3 km during the rut and 6.1 km during the post-rut, while female movement peaked following parturition at 3.3 km (Webb et al. 2010).

Region, weather, and other environmental conditions can also cause shifts in WTD movements. Under adverse temperatures, WTD may increase or restrict

movements to certain parts of the day to either conserve energy during more harsh conditions or expend energy during more favorable conditions. In more northern extents of the their range, WTD movements are primarily limited during winter months in response to low temperatures (Hoskinson and Mech 1976). Additionally, researchers found deer activity to increase during diurnal hours in response to lower temperatures (Ozoga and Gysel 1972). Furthermore, one Michigan study found most WTD movement activity to be correlated to temperatures between 10°C - 16°C during spring, summer, and autumn; with declines in activity at above or below the respective window (Beier and McCullough 1990).

As mentioned earlier, it is crucial that managers familiarize themselves with common movement patterns within a population of WTD. With the more recent outbreaks of chronic wasting disease (CWD) throughout many WTD populations in North America, data pertaining to movement rates within a particular population is specifically important in predicting potential vectors through which the disease can move across the landscape. By defining and documenting these movements within localized populations, biologists and managers can gain pivotal data in which to more accurately predict and prepare for disease transmissions should an outbreak occur.

Traditionally, there are three movement types that have been described and analyzed in WTD biology: dispersals, excursions, and migrations. Dispersals are the most heavily studied movement type. They are defined as a permanent movement from one home range to another (Kammermeyer and Marchinton 1976). Of the three movement types, dispersal has been the most heavily studied, however most biologists would agree that is still one of the least understood behaviors of WTD. While early studies concluded

that dispersal was thought to be mostly undertaken by adolescent males (Kammermeyer and Marchinton 1976, Nelson and Mech 1984), at least one early study from Illinois documented over 50% female dispersal (Nixon et al. 1991). Nonetheless, doe dispersal is still thought to be a rare occurrence because most studies on dispersal have documented males having much higher rates (Rosenberry et al. 2001, Nelson 1993, DeYoung 2011). Dispersal is believed to be a behavioral mechanism to avoid inbreeding (DeYoung 2011), with the motivation presumably stimulated by either increased competition during the rut (Rosenberry et al. 2001, Shaw et al. 2006) or maternal aggression during the spring fawning season (Holzenbein and Marchinton 1992). Dispersal distance is somewhat variable throughout literature, however there has been some correlation leading to the belief that individuals who undergo spring dispersals in attempts to avoid inbreeding move greater distances than those making the movements during the fall as a reaction to mate competition (Long et al. 2008).

Excursions are typically defined as temporary movements outside of an established home range in which the individual returns at a later time (Karns et al. 2011). While little is known about the motives behind these short movements, they are believed to primarily serve as function of the breeding season or occur in response to habitat variations (i.e. changes in food sources, variations in cover, human disturbances, etc.) (Karns et al. 2011). Like dispersals, excursions are typically thought of as a male dominant behavior which increasingly occurs during the rut. As multiple females enter estrous, males are likely to periodically "chase" unreceptive does from their respective home ranges (Richardson and Peterson 1974). When this occurs, there is an increased possibility for males to enter unfamiliar areas initiating aggressive interactions with other

bucks. Karns et al. (2011) found 63% of adult males made at least one excursion from their home range either immediately before or during the rut in Kent County, MD. Because individuals were highly unlikely to make repeat excursions to the same areas, most movements were not linked to food availability, but rather presumed functions of basic breeding behavior (Karns et al. 2011). As with dispersal, these movements should still be taken into management consideration, as they still play a vital role in the extent of genetic flow and possible disease spread across landscapes (Springer et al. 2016).

Seasonal migrations are defined as periodic movements from one region or climatic zone to another (Caughley and Sinclair 1994). Migrations differ from dispersals and excursions in that the individual will have two separate home ranges; revisiting each one at some point. These movements are also unique in comparison to others in that they are not ordinarily influenced by breeding behavior but rather by density independent factors (i.e. weather, habitat variations). Traditionally, these unique movements were believed to be undertaken only by northern WTD populations in response to harsh winter weather conditions (Verme and Ozoga 1971, Hoskinson and Mech 1976, Sabine et al. 2002). However, there have been documented cases of seasonal shifts in southern latitudes in response to habitat changes such as seasonal flooding (Byford 1970, Joanen et al. 1985). Migrations seem to be learned behaviors which are retained from a young age and are traditional in nature (DeYoung and Miller 2011). However, there is also evidence to support that fawns may rely on doe matriarchal groups to reach summer and winter home ranges (Nelson and Mech 1981, Teirson et al. 1985). Northern WTD herds will undergo seasonal migrations as a response to increased snowfall; relocating to areas which provide suitable canopy cover. These wintering areas or "yards" are typically

characterized by dense coniferous forests which serve as sheltering areas from dense snow packs and sub-zero wind chills (DeYoung and Miller 2011). Moreover, these areas also tend to provide herds with ample escape routes to avoid potential predators (Messier and Barrett 1985). Once the surrounding snowpack melts and temperatures begin to rise above freezing during diurnal hours, herds typically begin to return to summer ranges (Nelson and Mech 1986). Additionally, previous literature shows that the spring migrations are somewhat faster than fall migrations (Rongstad and Tester 1969).

URBANIZATION

Many urban communities were presumably absent of WTD until the 1970's or later (Bowman 2011). However, the growth and fecundity of urban WTD populations is now often one of the most concerning issues to managers. Urban areas can provide WTD with a plethora of suitable habitats which are often abundant with many sustainable food sources. WTD are considered an "edge" species; typically preferring transitional areas surrounded by a mosaic of different habitats which are directly adjacent to one another (VerCauteren and Hygnstrom 2011). Urban areas often encompass many "green spaces" (i.e. parks, arboretums, etc.) which act as habitat patches for WTD populations to utilize throughout the year (VerCauteren and Hygnstrom 2011). These areas also act as refugia for WTD which allow them to become acclimated to human interactions. Over time, WTD may transition deeper into urban areas which are often interspersed with appealing food sources (i.e. ornamental shrubberies, flowerbeds, gardens, etc.). Understandably, WTD populations have been known to cause a great deal of destruction to residential gardens and floricultural displays. Research suggests that in 2008 deer accounted up to $328 million in damage to metropolitan households in the United States (Conover 2011).

Another issue that continues to be a primary concern to managers involves deer vehicle-collisions (DVCs). Over 500,000 DVC's occur annually in the United States alone, however researchers suggest that only about half of the actual accidents are ever reported (Marcoux and Riley 2010, Romin and Bissonette 1996). Furthermore, multiple urban WTD studies have attributed DVCs to account for over 90% of documented mortalities (Etter et al. 2002, Storm et al. 2007).

Urban communities typically form along a gradient across the landscape; where habitat fragmentation increases as human development increases. Wildlife managers typically define the urbanization of an individual based on the number of homes or dwellings that are contained within its home range (Brown et al. 2005, Hansen et al. 2005). There are four urban categories which are commonly referenced within the literature: rural (0-5 homes/km^2), exurban (6-25 homes/km^2), suburban (25-250 homes/km^2), and urban (>250 homes/km^2).

Exurbia is characterized by its peripheries of human development which may be interspersed with agriculture or large residential lots (Bowman 2011, Hansen et al. 2005). Unlike urban and suburban lands, these areas often retain connectivity of suitable habitat patches for WTD (Odell and Knight 2001). In recent years, exurban areas have become an area of interest to WTD managers primarily due to their proximities to rural environments as well as their recent growth across the landscape (Storm et al. 2007). The total land area of exurbia in the United States has increased from just 5% in 1950 to over 25% in 2000 (Brown et al. 2005, Bowman 2011). Seasonal home range size is often highly variable within exurban WTD herds (Storm et al. 2007, Rhodes et al. 2010). However, annual home ranges tend to be more dependent on human development. Unlike

rural WTD who tend to be more cautious of areas containing heavy amounts of human development, exurban WTD have been shown to document shifts in seasonal habitat use towards developed areas (Storm et al. 2007, Bowman 2011). Movement patterns of WTD in exurbia tend to be consistent with other areas; being most active during crepuscular hours and least active during the day (Rhoads et al. 2010). Additionally, very little is known about the extent of specific movements such as dispersals and excursions in exurban environments. Conversely, wildlife managers should be urged to put more effort into research pertaining to WTD movements (such as dispersals and excursions) in exurbia. By developing management strategies in which to gage the levels of distance recolonization within these partially developed landscapes to reduce the effects of deer-human conflicts (Bowman 2011). Survivorship estimates within exurbia, while limited, are typically much higher than in rural landscapes. Storm et al. (2007) documented female annual survival as high as 87% in an exurban area of Southern Illinois.

Suburban landscapes are typically composed of a mixture subdivisions and homes which located on lots of variable sizes (Bowman 2011). While suburban WTD survival estimates tend to be higher than compared to rural WTD populations (Bowman 2011, Etter et al. 2002), DVCs typically increase with human development in these areas (Bowman 2011). These residential areas are often interspersed with dense woodlots and riparian corridors which act as refugia for WTD (Odell and Knight 2001). Deer tend to favor suburban environments due to higher qualities of available forage as well as decreased risks of predation or harvest (Bowman 2011). Residents of suburban communities are often either unaware or opposed to the use of hunting as a method of WTD population control. Suburban and urban WTD tend to have smaller annual home

ranges compared to exurban individuals (Kilpatrick and Sphor 2000a; Etter et al., 2002; Rhodes et al., 2010), however there are some discrepancies as to the extent variation among seasonal home ranges (Kilpatrick and Sphor 2000b, Etter et al. 2002). Movement patters of WTD in suburban areas are also somewhat variable. Grund (1998) reported changes in peak movement times among seasons; with WTD being more active at dawn during the winter, then shifting becoming more active at both dawn and dusk during the spring, and mostly active during nocturnal hours during the summer and fall (Grund et al. 1998). Again, there is a paucity of data pertaining to specific movements such as dispersals and excursions within suburban environments, however one foundational study by Etter et al. (2002) documented low levels of dispersal (>10%) for all cohorts apart from yearling males (50%) in suburban Chicago, Illinois.

Urban landscapes are characterized by high-density human development which include limited habitats separated by vast fragmentation, typically in the form of community parks or small, dense woodlots (Bowman 2011). These green spaces are often disconnected from one another; requiring WTD to move great distances from one suitable location to the next. Attitudes towards traditional population control methods (i.e. harvest, controlled sharpshooting) are often negatively perceived within urban areas due to lack of knowledge towards basic WTD ecology and management (Bowman 2011). While many studies have combined results for urban and suburban WTD populations, few have attempted to exclusively focus on urban WTD populations alone. Therefore, further research is needed to determine the extent of WTD population dynamics within true urban localities.

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CHAPTER 2

EFFECTS OF URBANIZATION ON THE SURVIVAL AND MOVEMENTS OF LOCALIZED POPULATIONS OF WHITE-TAILED DEER IN SOUTHERN INDIANA

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INTRODUCTION

Over the course of a century, the population dynamics of free ranging White-tailed deer (*Odocoileus virginianus*) (WTD) have changed across most regions of North America. Many populations were nearly extirpated from most of their native range during the early 20th century due to overharvest and excessive deforestation (McDonald and Miller 2004). Populations have since rebounded in most areas due to reintroduction efforts paired with comprehensive hunting regulations. These management strategies have allowed populations of WTD to grow exponentially (McCullough 1979), so much so, that by the early 1970s certain WTD densities had exceeded historical population levels (Alverson et al. 1988, Warren 1991, McShea et al. 1997, Adams and Hamilton 2011). By the 1990s, wildlife officials had begun implementing new management plans to limit the population growth of WTD in some urban communities (Messmer et al. 1997).

Urban communities frequently act as refugia for WTD populations (VerCauteren and Hygnstrom 2011). These areas are often absent of intense hunting pressure and typically have lower densities of natural predators than adjacent rural landscapes (DeNicola et al. 2000, Bowman 2011). They also provide WTD with an abundance of suitable browse, predominately ornamental shrubs and plants, which serve as food sources to sustain WTD throughout harsh winters (Kilpatrick and Spohr 2000). These habitat qualities are believed to greatly increase the reproductive success of WTD living within these areas. As a response to growing populations, urban WTD are often viewed as a nuisance by many landowners who have associated WTD with increased property damage from over browsing. These public perceptions are further supported with

increased deer-vehicle collisions (DVCs). Research suggests WTD account for as many as 1 million collisions per year (Conover 2011, Romin and Bassinette 1996, Marcoux and Riley 2010) with many urban WTD studies often attributing their highest form of mortality to DVCs (Etter et al. 2002, Porter et al. 2004). Despite the impact of DVC related WTD mortality, some suggest that urban WTD tend to exhibit higher levels of survivorship than rural WTD. For example, in suburban New York state, researchers observed female seasonal survival > 60% (Porter et al. 2004). Additionally, in suburban Chicago, Illinois, adult WTD of both sexes had annual and seasonal survival rates greater than 80% (Etter et al. 2002). However, it is important to note that these conclusions are drawn from studies which only focused on the survival of either urban or rural WTD populations or compare to data from a different location or time. Survival rates of WTD are highly variable across time and space (Anderson et al. 2015, DeYoung 2011). Therefore, the context of these results may be misleading because of the inherent high variability of survival date. There is a lack of data pertaining to the direct influence of urbanization on urban and rural WTD populations within the same general location and time.

While analyzing the effects of urbanization on localized WTD survival is critical, it is also important to quantity the influence urbanization has on seasonal movements as well. Seasonal movement patterns of WTD can play a huge role in the spread of infectious diseases such as chronic wasting disease (CWD) and bovine tuberculosis (TB) which can be detrimental to WTD herds. Moreover, these movements also can contribute to immigration and emigration which might influence population dynamics especially as they relate to management practices. Movements that potentially influence interactions

between localized populations include dispersals and excursions. Dispersals are typically defined as a permanent movement from one home range to another (Kammermeyer and Marchinton 1976). These movements generally occur during the late spring and early summer when maternal interactions are highest (Marchinton and Hirth 1984, Hölzenbein and Marchinton 1992) or during the fall when yearling males associate closely with older males throughout the rut (Hirth 1977, Ozoga and Verme 1985). Excursion movements are defined as temporary movements outside of an established home range in which the individual returns at a later time (Karns et al. 2011). These movements are often a common behavior of males during the fall breeding season when bucks pursue or "chase" receptive does outside their seasonal home ranges (Karnes et al. 2011, Hawkins and Klimstra 1970, Hölzenbein and Schwede 1989). Although these movements are considered fundamental in answering questions pertaining to population dynamics and implications of management decisions, they are still one of the least understood, yet typical behaviors of WTD (Diefenbach et al. 2008). As with survivorship, seasonal movements of WTD are highly variable. This is especially true when considering movement patterns between bucks and does across regional landscapes; as well as within localized populations of WTD along an urbanized gradient. Moreover, while few studies have analyzed these movement patterns within urban areas alone; no studies have attempted to quantify the influence of urbanization on localized WTD populations by comparing the movements of urban WTD, using an adjacent rural WTD populations as a control for annual variability.

While informative on a broad scale, all published survival and movement data were derived from studies confined to only one field setting (i.e., urban or rural) and can

only be compared to other studies which occurred at different places and times. Therefore, conclusions from each of these studies may not be able to truly isolate the effect of urbanization on localized WTD populations. By quantifying the influence of urbanization within localized populations of WTD, managers gain a more defined perspective of how dynamics vary within urban populations. In efforts to isolate and defined the effect of urbanization on WTD, we propose a direct analysis of these parameters, collected from both urban and rural landscapes within the same general location during the same period. By gaining a better understanding of the population dynamics within adjacent populations of urban and rural WTD, managers are provided with insights as to how urbanization effects WTD; therefore gaining a foundational basis for management decisions to be made.

STUDY AREA

This study took place in Monroe and Brown counties, southern Indiana USA. The primary focus for the urban portion of the study was in the greater Bloomington area, Monroe County, Indiana (Figure 1). The city has a fluctuating population that has been greater than 80,000 people since 2010. In 2016, the estimated population density of the city was approximately 1,400 people per/km^2. Total land area encompassing the city is 60.7km^2 and the highest elevation is 235 m. Habitat characteristics of rural study areas consists of agricultural croplands, open grasslands, and oak-hickory forests while urban study sites consist of small, fragmented, woodlots and grassy lawns. This research was conducted on both private and public lands, with the majority of public land confined to Morgan-Monroe and Yellowwood state forests.

METHODS

Capture and Handling Methods

We captured WTD using drop nets, Clover traps, and dart guns (Clover 1956, Ramsey 1968, Thompson, 1989). Deer were baited with a mixture of corn, peanut butter, and apples. Each WTD captured by clover trap, dropnet, and/or net gun received an initial intramuscular injection of 1-2 ml of butorphanol, azaperone, medetomidine (BAM, Wildlife Pharmaceuticals Inc., Windsor, CO) immediately after capture. When free darting, we remotely anesthetized WTD using specialized drug containment darts pre-filled with 2mL of BAM. Darts were affixed with specialized radio transmitter beacons (Pneu-dart, Inc., Williamsport, PA) which allowed us to track individuals after being darted. Dosages were based on manufactures instructions (Wildlife Pharmaceuticals Inc., Windsor, CO). All WTD were blindfolded to reduce stress and monitored for signs of full induction. Once WTD were anesthetized, we administered optic ointment to prevent corneal drying and either kept individuals sternal or placed them in lateral recombency on their left side to reduce bloat. We then estimated age by using tooth eruption, and wear (Severinghaus 1949). Each WTD was then equipped with either a global positioning system (GPS) collar (G2110E Iridium, Advanced Telemetry Systems Inc., Isanti, MN) or very high frequency (VHF) collar (M2230B, Advanced Telemetry Systems Inc., Isanti, MN). Collars were sex specific with buck collars including an integrated elastic, neoprene band to compensating for neck growth during the rut. Individuals were either intramuscularly or intravenously injected with reversal doses of both atipamezole and naltrexone to antagonize the effects of BAM. All capture and handling methods were conducted in accordance with the Institutional Animal Care and Use Committee at Ball

State University (IACUC Protocol #: 648052-2)

Monitoring Movements

Each GPS collar was pre-programmed to obtain four locations per day at 0100, 0700, 1300, and 1900 hours. Individuals fitted with VHF collars were manually located two to four times weekly using radio telemetry equipment. We attempted to obtain locations by "homing-in" on VHF collared individuals with the use of vehicle-mounted 5-element and handheld 3-element Yagi antennas (Wildlife Materials Inc., Murphysboro, IL) and receiver (R2000, Advanced Telemetry Systems Inc., Isanti, MN). Each location was determined by visual confirmation or by triangulation techniques using azimuth bearings. Bearings were only recorded if intercepting angles were between 30° and 150°. Telemetry error was determined in LOAS (Ecological Software Solutions LLC, Hegymagus, Hungary) which resulted in a 5.49 ha average error ellipse.

Mortality Investigation and Survival Analysis

In order to investigate potential mortalities, both GPS and VHF collars were set to transmit a unique pulse rate after four hours of inactivity (i.e., mortality signal). Additionally, GPS collars sent a notification email once a mortality was detected which included the last location acquired by the collar. Once a mortality signal was received, the carcass was located with radio-telemetry and a field necropsy or site investigation was conducted to determine specific cause of death (O'gara 1978, Chitwood et al. 2014, White et al. 1987). Similar to Anderson et al. (2015), we categorized mortalities into one of 5 categories: deer vehicle collision (DVCs), hunter related, predator, accident, and unknown. We censored for capture myopathy if mortality occurred ≤ 14 days post

capture (Harthoorn 1977, Chalmers and Barrett 1982, Rongstad and McCabe 1984, Nelson and Mech 1986, Pond and O'Gara 1994, DelGiudice et al. 2005).

Survival was estimated by using the known-fates model to determine annual and seasonal survival rates for male and female WTD (Anderson et al. 2015, Kaplan & Meier 1958, Laake 2013, Papadatou et al. 2011). We devised 8 *a priori* models to determine the influence of locality (urban or rural), season (Summer, fall/winter, and winter/spring), and sex (M = male, F = female) on survival (Table 1). To obtain seasonal survival estimates, we divided the study period into three seasons: summer (15 May–30 Sep), fall/winter (1 Oct–15 Dec), and winter/spring (16 Dec–14 May) (Nixon et al. 1991, Anderson et al. 2015). For each season, survival rates were expotentiated by the number of 2-week intervals within the season to yield full-season survival rates. Additionally, annual survival rates were calculated by multiplying full-season survival rates (White 1999, Anderson et al. 2015). Parameters of the model were estimated using Bayesian inference.

Home Range Estimation and Classification of Urbanization

Locations for collared WTD were imported into ArcGIS software (Pacer, Truro, Nova Scotia, Canada). Seasonal movements of GPS collared deer were analyzed after creating 95% fixed kernel density estimate (KDE) home ranges in ArcGIS. All WTD equipped with VHF collars had reduced location samples compared to those equipped with GPS collars therefore falling below the recommended minimum of 30 locations per season needed to accurately represent a seasonal home range using the KDE method (Seaman et al. 1999, Girard et al. 2002). Therefore, we only used VHF collared WTD for

permanent relocation movements (dispersals) analysis. We determined the urbanization zone of WTD based on parcel estimates obtained from local officials within the city. Parcel layers were overlaid on top of 1km buffers of home ranges in ArcGIS to determine the number of residences which were contained within each home range. We considered WTD to be urban/suburban if their home range buffers contained ≥26 homes per km^2 (i.e. urban/suburban; here after urban) and rural/exurban if buffers contained <26 homes per km^2 (i.e. exurban/rural; here after rural) (Brown et al. 2005, Hansen et al. 2005).

Dispersal

Movements were defined as dispersals when an individual emigrated from its original home range and was not located again within that original area (Anderson et al 2015, Anderson 2010, Stenseth 1992). Due to time between recording locations, we did not consider excursions from VHF collared deer. Home ranges analyzed for dispersal were used only if WTD were located for a minimum of 30 unique days. Dispersals were determined by observing point data in chronological order. Bayesian analysis was used to estimate dispersal rates using the known fates survival model; treating the dispersal event as if it were a mortality (Anderson, 2015).

Excursions

Excursions were defined as temporary movements (lasting ≥ 6 hours) of at least 0.5 km from an established home range (Karns et al. 2011). Excursion distances were measured from the closest 95% contour line of each of the individual's seasonal home range to the furthest obtained location. Final distances were measured from home ranges that were established after excursion movements were removed. Distances were

measured using the near tool in ArcGIS. To alleviate data loss due to mortality or collar failure, we included all seasonal excursions from WTD which retained their collar for at least 60% of the season. Additionally, points for each movement had to begin and end within the 95% home range polygon before they were included in the analysis. To differentiate obvious excursions from extraneous extensions of the home ranges (movements included within disconnected portions of home range polygons), we classified excursions from home ranges if they fell within a random extension of a home range that was visited less than three times, in which each visit lasted less than 48 hours (96 hours total), we still considered the points as excursions if they were still greater than 0.5 km away from the primary home range polygon. We used occupancy modeling to determine excursion probabilities at any given two-week interval using locality (urban/rural), season (winter/spring, summer, fall/winter), and sex (M/F) as covariates of detection. Typically, the occupancy modeling framework is used to estimate presence or absence of species within a habitat; with occupancy (analogous to excursion) and detection (analogous to excursion probability) the two parameters of estimated. The primary interest of this research is the detection parameter which describes the probability a deer will make an excursion in a two-week interval. Parameters of the occupancy model were estimated using Bayesian inference.

Modeling Methodology

We conducted all analyses under Bayesian inference in Program R (R Core Team 2014) using JAGS; a program designed for Bayesian analysis of hierarchical models which uses Markov Chain Monte Carlo (MCMC) simulation to obtain posterior distributions across a dataset (Plummer 2003). Each of the parameters used within our

analyses were given vague prior probability distribution. We ran three congruent MCMC chains using 5000 saved steps, thinning every three steps, and discarding the first 1000 steps. We determined convergence of the MCMC chains by using Brooks-Gelman-Rubin (BGR) scale-reduction factor. This is essentially the ratio between-chain variability to within-chain variability at which MCMC chains converge closer to one (Brooks and Gelman 1998). All BGR statistics for our analyses were less than 1.10 indicating convergence. We used deviance information criterion (DIC, Spiegelhalter et al. 2002) to rank and determine the most parsimonious models within each analysis. The model ranked with the lowest ΔDIC value was considered the most parsimonious and was therefore used to draw inferences. This ranking process allows for a better explanation of variations within the data set while still using the smallest number of parameters to do so (Papadatou et al. 2011). All posterior distributions were presented as medians with 95% credible intervals in parentheses.

RESULTS

Between January 2015 to July 2016, a total of 85 unique WTD was captured from the study area consisting of 40 rural individuals (M = 20, F = 20) and 45 urban individuals (M = 25, F = 20) with an average number of homes/km^2 for urban WTD at 582.76 (range: 39-1162) while the rural WTD averaged 6.33 (range: 0-24). Additionally, at the conclusion of the 2016 field season, final sample size was evenly distributed among sex (M/F), locality (urban/rural), and collar type (GPS/VHF). However, we were forced to censor some individuals from analyses (n =15) due to unforeseen poor collar retention (primarily GPS buck collars).

Cause-Specific Mortality and Survival

A total of 32 WTD died during the study. We censored 4 individuals for capture myopathy, with all but one instance occurring ≤ 72 hours post capture. Of the remaining mortalities, 18 (M = 12, F = 6) were urban and 11 (M = 5, F = 6) were rural (Figure 2). Primary cause of mortality among urban WTD was attributed to DVC's (*n* = 10) whereas rural WTD mortality was predominantly hunter related (*n* = 8). Accidents (*n* = 4) were also a significant form of mortality among urban WTD, as individuals were struck by train (*n* = 2), impaled by rod iron fence (*n* = 1), and presumably died of exhaustion after having antlers entangled within a tree (*n* = 1). As expected, with non-neonate WTD (> 6 months of age) predation (*n* = 1) was low. From the 85 WTD that were captured, a total of 77 was included in the survival model. We censored remaining WTD from analysis due to capture related mortalities (*n* = 3) and collar failure (*n* = 5) which all occurred ≤ 4 days post capture. Our best fit model incorporated both sex and season but did not include location (urbanization) as an important predictor of survival (Table 2). Survival rates for two-week intervals were virtually identical for both sexes aside from a slight drop for males during the fall/winter season (M = 0.94, 95% CI [(0.90 - 0.97], F = 0.97 - 95% CI [0.95 - 0.99]). Seasonal survival rates were lowest for both sexes during the fall/winter (M = 0.51, 95% CI [0.31 - 0.70], F = 0.97, 95% CI [0.95 - 0.99]) however females had higher rates across all seasons (Table 3). Additionally, female WTD had much higher annual survival (F = 0.62, 95% CI [0.43 - 0.79]) compared than males (M = 0.31 - 95% CI [0.16 - 0.50]).

Seasonal Movements

Only 8 of 74 unique WTD made dispersals from established home ranges. All dispersals were made by males (urban = 5, rural = 3). Timing of dispersals occurred across all seasons (winter/spring=2, summer=3, fall/winter=3). Our best fit model for dispersal indicates there were differences between sex (M_3, Table 4). Both two-week interval and annual dispersal were much lower for females than males (Table 5). A total of 85 seasonal excursions were observed from a total of 27 WTD equipped with GPS collars during the 2016 sample year. As expected, the highest number of excursions occurred during the fall/winter season (n = 33). Our best fit occupancy model included locality and season as predictors but not sex (M_6; Table 6). Rural WTD had higher excursion probabilities across all seasons compared to their urban counterparts. Moreover, excursion rates were considerably higher for WTD from both localities during the winter/spring and fall/winter seasons compared to the summer (Table 7). Average distance of excursions was similar for both localities (rural = 2.52 km ± 0.56; urban = 2.43 km ± 0.70).

DISCUSSION

Survival and Cause-Specific Mortality

Surprisingly, our data indicate that urbanization was not correlated with survival. Our predictions of annual and seasonal survival were lower than previously reported among adult WTD in suburban and rural areas of Illinois (Nixon et al. 1991, Anderson et al. 2015). As with Anderson et al. (2015), we reported on pooled survival rates of both sexes which includes that of both yearlings and older aged individuals. Our study also reports DVC numbers similar to previous urban/suburban studies in that they accounted

for > 55% of urban WTD mortality (Etter et al. 2002, Lopez et al. 2003). Furthermore, DVC's did not account for any rural WTD mortalities in our study. We also observed hunting related mortality similar to previous studies; accounting for >70% of all rural WTD mortalities within our study (Storm et al. 2007, Ebersole et al. 2007, Nixon et al. 1991). It should also be noted that while archery hunting was allowed within the urban city limits, instances of hunting related mortality within the urban area were rare (n = 1). This was presumably linked to negative public perception towards hunting within urban areas, challenges of hunting small parcels and fear of hunting related accidents (Bowman 2011).

Our results support the conclusion that survival rates vary depending on the season and sex of the individual. Previous studies have also reported similar decreases in survival rates of males during the fall/winter season (Anderson et al. 2015, Nixon et al. 1991, VanDeelen et al., 1997). These results are not surprising in that our fall/winter season coincides with legal hunting activities; hence males having lower survival during this time could presumably be linked to hunter bias toward bucks (i.e., antlered deer). Furthermore, it is important to note that hunters may have more observations of bucks during the fall due to increased movement rates associated with the breeding season (Karns et al. 2011). However, our results indicate a more balanced sex ratio for hunter related mortality (55% male, 44% female); suggesting that there are other factors contributing to higher survival of females associated with fall hunting seasons. All but one (1) hunter related mortality occurred during the months of November; with the primary method being modern firearm. These results were expected as Indiana firearms hunters accounted for over 59% and 65% of total harvested WTD during 2015 and 2016

respectively (Caudell and Vaught 2017). Males accounted for 70% of WTD killed by DVCs within our study. This imbalance is not uncommon as other Midwestern studies have also observed higher rates of male DVCs (Nixon et al., 1991). As with hunter harvest, sex specific differences of DVCs could also be presumably linked to higher movement rates of males; more specifically during the fall. Unfortunately, most states (including Indiana) do not obtain sex specific data for reported DVCs; hence further research is needed to confirm that males are more likely to be killed by DVCs than females.

Seasonal Movements

Based on our data, dispersal rates were not related to urbanization while excursion rates likely were. This relationship between urbanization and decreased excursion probability was evident across all sampling seasons and sex made no difference in our predictions. The influence of urbanization on excursion rates of localized populations is presumably linked to unique habitat characteristics that encourage WTD to move less outside seasonal home ranges due to higher quantities of available browse (Kilpatrick and Spohr, 2000). The threat of predation on adult WTD within urbanized areas is likely non-existent or very low; hence adult WTD are not normally chased from home ranges within these areas. These results reinforce the hypothesis that adult WTD within these areas have a lesser need to venture from seasonal home ranges in order to survive; therefore, once a seasonal home range has been established movements are rare. Trudeau et al. (2017) found that urban does in Bloomington had much smaller home ranges and core areas than urban males, therefore this behavior could be a result of home range overlap and resource competition due to overcrowding (Trudeau et al. 2017).

Urbanization and season where not significant in predicting dispersal rates. Dispersal rates in our study were reflected as a male dominant behavior in that annual dispersal rates were 0.261 for males and < 0.001 for females. Nonetheless, our study reports results which are congruent with previous dispersal rates for other urban/suburban populations of WTD. Etter et al. (2002) observed similar dispersal rates for males in suburban Chicago at 0.22 for bucks, whereas doe dispersal was only 0.07. However, the timing of urban/suburban dispersals were primary during the spring and thought to be brought on by maternal aggression (Etter et al., 2002). Conversely, the timing of dispersals within our study occurred sporadically throughout the year (winter/spring=2, summer=3, fall/winter=3). Although highly speculative, dispersals in urban/suburban areas could be influenced by preference of available food resources which are commonplace within these settings. Numerous landowners within our urban/suburban study area would often supply feed year-round in efforts to attract WTD on to their property for aesthetic reasons. Hence, it may be possible to entice WTD to remain within a particular area for extended periods of time without returning to a previous home range.

In addition to urbanization, excursion rates were also related to season within both locations. Or results indicate that seasonal changes in excursion rates are similar between urban classes within localized populations; with increases in excursion rates during the fall/winter and winter/spring seasons. Within our study, over 87% of GPS collared WTD analyzed in our excursion analysis made at least one seasonal excursion throughout our 2016 sampling year and all WTD (both urban and rural) were more likely to be observed on an excursion during the winter/spring and fall/winter compared to the summer. The relationship between seasonality and excursion rates are consistent with previous

literature. From 2003-2007, Karns et al. (2011) observed excursions from fall/winter home ranges by adult males. The majority of these excursions (73%) occurred from Oct. 4-Dec.16, which were similar to the dates used in our fall/winter analyses (Karns et al., 2011). Additionally, we also observed higher excursion rates during the fall/winter season, with more individuals being tracked (40% urban , 60% rural), but under a shortened sampling window compared to the other two seasons.

MANAGEMENT IMPLICATIONS

The influence of urbanization on WTD population dynamics should always be considered during the implementation of management actions, especially when applications are designed with the purpose of altering localized populations of WTD living along an urbanized landscape gradient. Surprisingly, our results indicate that the influence of urbanization affects populations differently on a localized scale; suggesting that while urban WTD may be more sedentary than their rural counterparts, overall survival rates are similar. Therefore, this study serves to encourage WTD managers to consider urban and rural WTD populations independently. Coupling this with results from a previous study by Williamson et al. (2015), WTD fawns reaching at least 17 weeks of age in urban Bloomington exhibited survival rates >90% as a relation to increasing densities of homes while those in rural/exurban landscapes just outside the city were much lower (>40%). Therefore, localized populations of urban WTD in southern Indiana are presumably experiencing higher levels of recruitment while retaining similar levels of adult survival with those WTD in more rural areas. If management goals are centered on reducing urban WTD populations, our study would suggest focusing applications on urban does. While our models indicate no difference in survival rates

between urban and rural WTD, it is still important to consider the ramifications of cause specific mortality in these areas. Managers should be mindful of the impact of DVCs within urban areas and consider implementing programs to encourage control methods within areas which may be more susceptible to accidents. Our research would urge agencies to consider combinations of management applications (lethal and non-lethal) which serve to micro manage urban WTD within localized populations. Working in conjunction with recruitment reducing measures in does, strategic lethal removal of bucks could synergistically expedite management in urban areas by removing those individuals which may already be at higher risk of being in struck by vehicles. Additionally, combinations of lethal and non-lethal applications such as these may bring balance to negative public backlash by reaching realistic compromises with citizens who may have emotional connections towards the well-being of urban WTD.

We found that urban WTD moved from home ranges less than their rural counterparts regardless of season. These more sedentary WTD are less likely to spread CWD or other infectious diseases across the landscape. At least for southern Indiana, our data would suggest prioritizing management approaches towards more rural populations should an outbreak occur. Our results aim to encourage managers to become aware of periods of the year when WTD populations could experience an accelerated spread of infectious diseases, more specifically from October-May (fall/winter and winter/spring seasons) and to develop protocols which will focus primarily within areas where WTD are the least sedentary. Further research is needed to determine what types of transitional zones act as funnels to and from urbanized portions of the population. This could provide managers with a better understanding of how movement pathways act as potential vectors

of disease outbreaks along an urbanized landscape gradient. Therefore, managers should consider conducting habitat analyses which quantify space usage of WTD moving to and from urbanized areas.

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Figure 1: Inset map of the city of Bloomington and Monroe and Brown counties, southern Indiana, USA

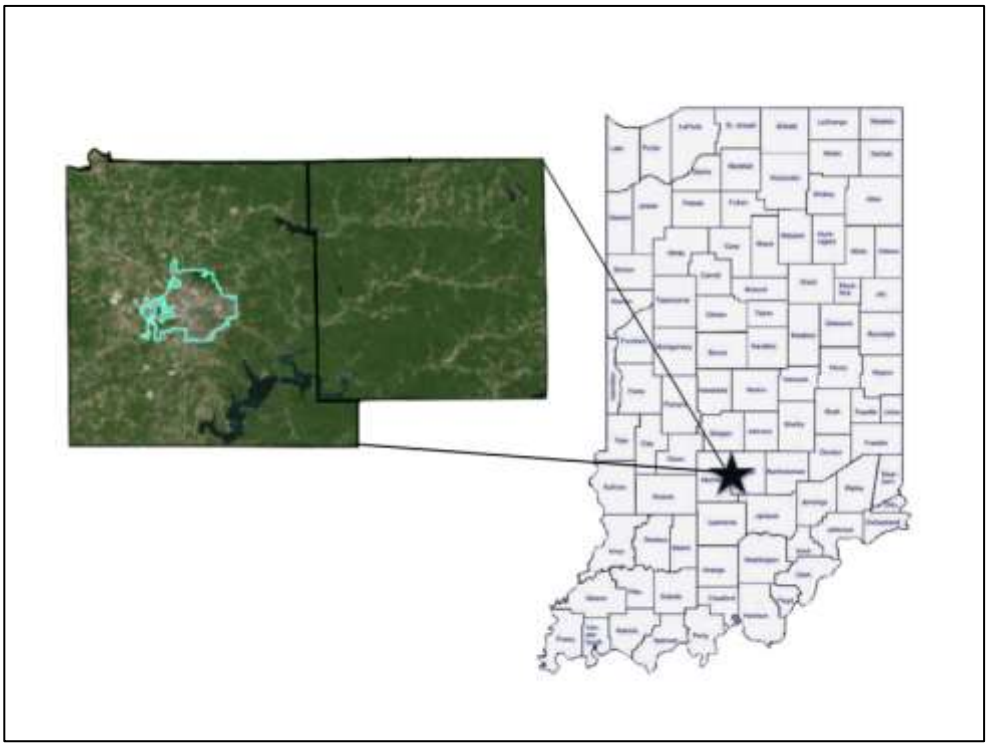

Figure 2: Cause-specific mortality of urban and rural WTD in southern Indiana, USA. 2015-16

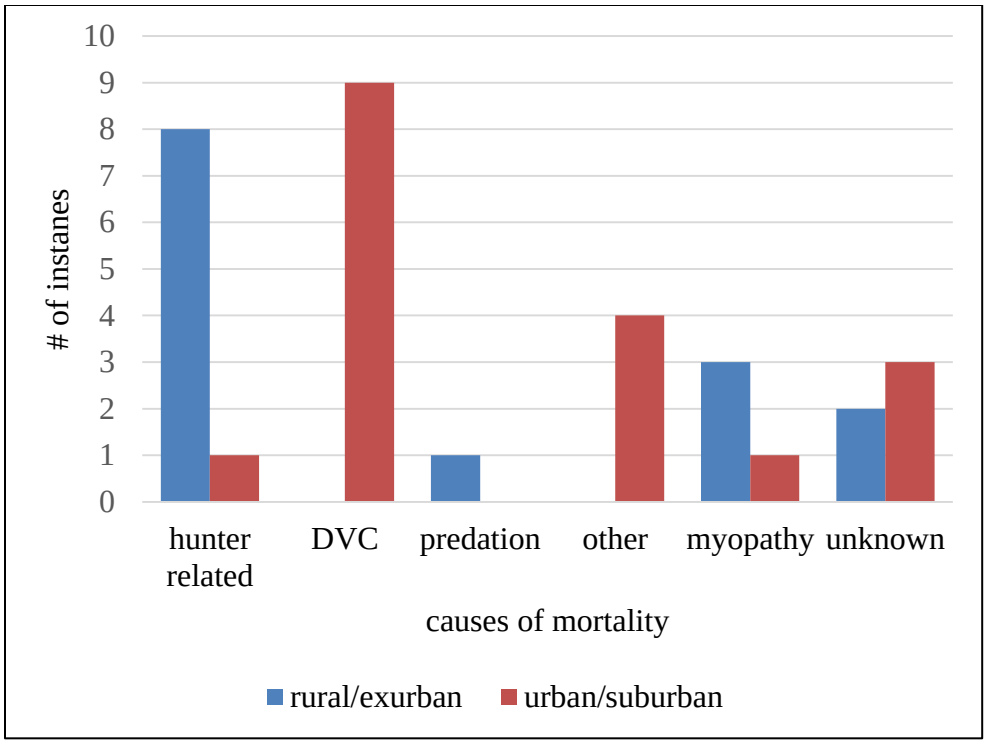

Table 1: *A priori* models used to estimate survival, dispersal, and excursion rates of WTD in southern Indiana, USA, 2015-2016

model	K^a	description
M_1	1	remains constant (null model)
M_2	2	varies by location (urban/suburban; rural/exurban)
M_3	2	varies by sex (F = female, M = male)
M_4	3	varies by season (summer, fall/winter, and winter/spring)
M_5	4	varies by location and sex
M_6	6	varies by location and season
M_7	6	varies by sex and season
M_8	12	varies by locality, sex, and season

[a] number of parameters estimates

Table 2: Top models for predicating survival of urban and rural WTD in southern Indiana, USA, 2015-16. (DIC = deviance information criterion)

model[a]	ΔDIC	description
7	0.0	varies by season and sex
8	2.2	varies by season, sex, and location
4	3.1	varies by season
6	5.4	varies by season and location
3	13.3	varies by sex
5	15.3	varies by sex and location
1	16.4	remains constant (null)
2	18.4	varies by location

[a] models defined in table 1

Table 3: Estimated seasonal survival rates of urban and rural WTD in southern Indiana, USA, 2015-16. (95% credible interval).

	female		male	
season	2-week interval	full season	2-week interval	full season
fall/winter	0.97 (0.95-0.99)	0.76 (0.59-0.88)	0.94 (0.90-0.97)	0.51 (0.31-0.70)
summer	0.99 (0.99-1.00)	0.90 (0.78-0.96)	0.99 (0.97-0.99)	0.78 (0.58-0.91)
winter/spring	0.99 (0.99-1.00)	0.91 (0.79-0.97)	0.99 (0.97-1.00)	0.80 (0.59-0.93)

Table 4: Top models for predicating dispersal of urban and rural WTD in southern Indiana, USA, 2015-16. (DIC = deviance information criterion)

model[a]	ΔDIC	description
3	0.0	varies by sex

5	2.2	varies by sex and location
7	3.2	varies by season and sex
8	4.9	varies by season, sex, and location
1	13.8	remains constant (null)
2	15.6	varies by location
4	16.8	varies by season
6	18.6	varies by season and location

[a] models defined in table 1

Table 5: Estimated annual dispersal rates of male and female WTD in southern Indiana, USA, 2015-16. (95% credible interval)

sex	2-week interval	annual rate
female	< 0.001	0.005 (0.001-0.046)
male	0.012 (0.005-0.022)	0.261 (0.126-0.433)

Table 6: Top models for predicating excursion probability of urban and rural WTD in southern Indiana, USA, 2015-16. (DIC = deviance information criterion)

model[a]	ΔDIC	description
6	0	varies by season and location
8	1.6	varies by season, sex, and location
4	2.4	varies by season
7	4.1	varies by season and sex
2	9.8	varies by location
1	11	remains constant (null)
5	11.7	varies by sex and location
3	12.8	varies by sex

[a] models defined in table 1

Table 7: Seasonal excursion probabilities of WTD from different localities in southern Indiana, USA, 2016 (95% credible interval)

season	rural/exurban	urban/suburban
fall/winter	0.27 (0.19-0.37)	0.17 (0.10-0.26)
summer	0.13 (0.08-0.19)	0.08 (0.04-0.12)
winter/spring	0.32 (0.20-0.46)	0.20 (0.13-0.30)